



Review Article

Insecticide Resistance Status, Mechanism and Control Measures of Dengue Vector *Aedes aegypti*: A Systematic Review

M. A. Habib Siam✉, D. Dey, and J. K. Owaresat

Department of Zoology, University of Chittagong, Chittagong- 4331, Bangladesh.

ARTICLE INFO	ABSTRACT
Article history Received: 12 March 2026 Accepted: 24 September 2026 Published: 30 September 2026 Keywords <i>Aedes</i>, Mosquitoes, Insecticide, Resistance, Control Correspondence M. A. Habib Siam ✉: ahashan.siam@gmail.com OPEN ACCESS	<i>Aedes aegypti</i> is a primary vector responsible for transmitting several public health-threatening diseases, including dengue fever, urban yellow fever, chikungunya, and Zika virus. Vector control has traditionally relied heavily on various chemical insecticides; however, this prolonged and intensive use of synthetic chemicals has led to the development of insecticide resistance in mosquito populations. This review outlines the current status of resistance develops to key classes of chemical insecticides, including carbamates, organochlorines, organophosphates, and pyrethroids. Additionally, the review provides an in-depth explanation of the underlying mechanisms responsible for the resistance observed in <i>Aedes</i> mosquitoes in natural populations. Four main types of resistance mechanisms have been identified based on biochemical processes, including Altered target-site resistance, Metabolic resistance, Penetration resistance and Behavioral resistance. This study reveals that <i>Aedes aegypti</i> demonstrates the highest resistance to pyrethroids, especially permethrin and deltamethrin, yet remains comparatively susceptible to organophosphates, notably malathion and fenitrothion. Further research is necessary to address key knowledge gaps and support the development of effective alternatives to conventional insecticides. It is suggested to exploit the effectiveness of plant-based compounds, biological control agents, and sterile insect technique to control the <i>Aedes aegypti</i> population.
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Introduction

Aedes mosquitoes are major vectors responsible for spreading dengue, chikungunya, yellow fever, and Zika viruses. (Smith et al., 2016). Over the past 50 years, dengue cases have surged by 30 times. It is now estimated that 50 to 100 million infections occur each year across more than 100 endemic countries, placing nearly 4 billion people at risk (WHO. 2024). Originally native to Africa, *Aedes aegypti* has since spread to southern parts of North America, Central and South America, Southeast Asia, the Middle East, the Pacific and Indian Islands, northern Australia, and occasionally parts of Europe (Mousson et al., 2005).

According to Shafique et al., (2019), current methods for controlling disease vectors are generally categorized into three types: environmental, chemical, and biological. Environmental measures include wearing long-sleeved clothing, using bed nets, and covering water-holding containers like tires and jars. Chemical measures involve using mosquito coils, repellents,

insecticidal sprays, and larvicides like temephos. Biological control methods use agents such as *Bacillus thuringiensis israelensis*, guppy fish, and sterile insect techniques (Hamaed et al., 2022). In the absence of specific drugs or vaccines to treat dengue or dengue hemorrhagic fever, the only effective way to prevent the spread of the disease is by controlling its vector. Since their discovery, insecticides have been extensively used for mosquito control (Kongmee et al., 2004). There are four main types of insecticides commonly used for controlling mosquitoes, such as- pyrethroids, organophosphates, carbamates, and organochlorines (Moyes et al., 2017). However, the frequent and extensive use of insecticides has led to the development of resistance in vector mosquitoes (Sipin et al., 2021). The widespread development of insecticide resistance in mosquito populations has renewed interest in the application of neonicotinoid insecticides for mosquito control (Paul et al., 2006; Pridgeon et al., 2008). Among these, imidacloprid ((E)-1-(6-chloro-3-pyridinylmethyl)-N-nitroimidazolidin-2-

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ylideneamine) is a neonicotinoid that acts by binding to nicotinic acetylcholine receptors in the insect nervous system, ultimately disrupting normal nerve transmission (Tomizawa and Casida, 2005). Gaining a comprehensive understanding of insecticide resistance and its underlying mechanisms is essential. This systematic review aims to analyze the insecticide resistance status of *Aedes* mosquitoes, explore the underlying resistance mechanisms, and identify potential management strategies for controlling *Aedes aegypti*.

Material & methods

This study utilized a systematic review approach, where a comprehensive literature search was conducted through online databases such as PubMed, ScienceDirect, Google Scholar, and Scopus to find articles related to insecticide resistance in *Aedes aegypti*. Keywords used in the search included: "insecticide resistance," "insecticide susceptible," "insecticide exposure," "pyrethroid resistance," "organochlorine resistance," "organophosphate resistance," "carbamate resistance," "resistance mechanism," and "Aedes." The resistance status (high, moderate, low, or susceptible) reported in this review was extracted directly from the respective original studies based on the criteria and interpretation adopted by each study and was not reclassified by the authors. Only peer-reviewed articles published in English between January 2010 and June 2026 were considered for inclusion in this review.

This systematic review included studies that met the following criteria:

1. Target Species: Studies focusing exclusively on resistance of *Aedes aegypti* mosquitoes.
2. Insecticide Classes: Research that evaluated resistance to any of the following insecticide classes: pyrethroids, carbamates, organophosphates, or organochlorines.
3. Resistance Mechanisms: Studies reporting on the underlying mechanisms of resistance, including but not limited to target site mutations (e.g., kdr mutations), metabolic detoxification (e.g., elevated enzyme activity), penetration resistance, or behavioral resistance.
4. Control Strategies: Articles that discussed or evaluated only *Aedes* vector control strategies in response to observed resistance.
5. Study Types: Peer-reviewed original research articles, including laboratory bioassays, field-

based resistance surveillance, and molecular studies on resistance mechanisms.

6. Language: Only studies published in English were considered.

Overview of insecticides used against *Aedes aegypti*

Chemical insecticides play a crucial role in controlling *Aedes* species through methods such as space spraying, insecticide-treated materials, larvicides, and residual spraying (Roiz et al., 2018). Five primary classes of chemical insecticides— pyrethroids, organochlorines, organophosphates, carbamates, and neonicotinoid — have been widely utilized across the globe to control dengue vector *Aedes aegypti*.

Organochlorines

Organochlorines are chlorinated hydrocarbons that were developed in the 1940s, with dichlorodiphenyltrichloroethane (DDT) being the most well-known and widely used insecticide from this group (Gerba, 2019). These compounds are recognized for their high toxicity, persistence in the environment, and tendency to bioaccumulate. However, they have been largely banned in developed countries due to their excessive and harmful use (Jayaraj et al., 2016).

Organophosphates

Organophosphates are regarded as less environmentally persistent compared to organochlorines, which is why the WHO still recommends them for vector control (WHO, 2022). Originally developed as nerve agents during World War II, their effectiveness as insecticides was identified soon after (Grue et al., 1997). For the past 20 to 30 years, Organophosphate's insecticides such as temephos (used as a larvicide) and malathion (used as an adulticide) have been the primary tools for controlling *Aedes aegypti* mosquitoes and preventing dengue in Caribbean member countries (Rawlins and Wan 1995).

Carbamates

Carbamate insecticides come from carbamic acid and include common types like carbaryl, carbofuran, propoxur, and aldicarb. They work in a similar way to organophosphates by blocking the enzyme acetylcholinesterase (Heckel, 2012). However, their effects are usually easier to reverse, so insects might recover if they're only exposed to small amounts (Dent, 2000; Gupta, 2019). Additionally, carbamates have relatively short-lasting toxicity because the carbamylated serine residue is unstable (Darvesh et al., 2008).

Pyrethroids

The fourth group is made up of pyrethroids, which are the newest class of insecticides and were first introduced to the market in 1980 (Melo-Santos et al., 2010; Klaassen, 1996). Due to their higher potency, longer environmental persistence, and lower toxicity to mammals, pyrethroids remain the most commonly used insecticides, especially in dengue-endemic regions (Siti-Futri et al., 2020). Pyrethroid insecticides are now widely used around the world to control adult *Aedes aegypti* mosquitoes. They make up about 17% of the global insecticide market and account for roughly \$1.4 billion in international trade (Housset & Dickmann, 2009). The most commonly used pyrethroids include deltamethrin, cypermethrin, cyfluthrin, lambda-cyhalothrin, metofluthrin, permethrin, d-allethrin, alpha-cypermethrin, pyrethrum, bifenthrin, d-phenothrin, z-cypermethrin, and etofenprox. These are typically applied through either residual treatments or space spraying (Kasai et al., 2014, Smith et al., 2016).

Neonicotinoid

The extensive and indiscriminate use of pyrethroid insecticides has promoted the evolution of resistance in mosquito vectors while also posing risks to aquatic ecosystems (Kumar et al., 2009; Luo and Zhang, 2011). As a result, alternative insecticides with novel modes of action, including neonicotinoids, have been developed to replace pyrethroids. Neonicotinoids generally exhibit low toxicity toward mammals and many non-target organisms, making them promising alternatives for effective mosquito control (Tomizawa and Casida, 2005). Imidacloprid and other neonicotinoid insecticides, when applied alone or in combination with conventional insecticides, have proven effective against pyrethroid-resistant mosquitoes, highlighting their potential role in resistance management strategies (Darriet and Chandre 2013; Paul et al., 2006). However, the unregulated and frequent use of insecticides over time has resulted in the development of resistance in mosquitoes (Table-1, Figure-1).

Table-1. The outcome of different types of insecticides used against *Aedes aegypti* throughout the world.

Sl. No	References	Location	Insecticide name	Insecticide class	Findings
01	Konkon et al., 2026	Benin	Permethrin Deltamethrin Bendiocarb	Pyrethroid Pyrethroid Carbamate	High Resistance High Resistance Susceptible
02	Piedra et al., 2026	Cuba	Temephos	Organophosphate	Susceptible in Las Tunas; Moderate resistance in Cienfuegos, and Sancti Spiritus; High Resistance in Pinar del Rio
03	Mahyoub et al., 2026	Saudi Arabia	Lambda-cyhalothrin Permethrin Cyfluthrin Malathion Fenitrothion	Pyrethroid Pyrethroid Pyrethroid Organophosphate Organophosphate	Moderate Resistance Moderate Resistance Moderate Resistance Moderate Resistance High Resistance
04	Haidy Massa et al. 2025	Mauritania	Permethrin Deltamethrin Bendiocarb Malathion Temephos	Pyrethroid Pyrethroid Carbamate Organophosphate Organophosphate	High Resistance High Resistance High Resistance High Resistance Susceptible
05	Singh et al. 2025	Uttarakhand, India	Temephos	Organophosphate	Moderate Resistance
06	Ng, & Zuharah, 2024	Malaysia	Deltamethrin	Pyrethroid	High Resistance
07	Che-Mendoza et al., 2023	Mexico	Permethrin Clothianidin	Pyrethroid Neonicotinoid	High Resistance Susceptible
08	Zulfa et al. 2022	Singapore and Cambodia	Permethrin Deltamethrin Malathion	Pyrethroid Pyrethroid Organophosphate	High Resistance High Resistance Susceptible
09	Ninditya et al. 2022	South Sumatra, Indonesia	Malathion Deltamethrin Permethrin Lambda-Cyhalothrin Cyfluthrin Bendiocarb	Organophosphate Pyrethroid Pyrethroid Pyrethroid Pyrethroid Carbamate	Susceptible High Resistance High Resistance High Resistance Moderate Resistance Moderate Resistance
10	Rahman et al. 2021	Lahore, Pakistan	Permethrin Deltamethrin Malathion Temephos	Pyrethroid Pyrethroid Organophosphate Organophosphate	High Resistance High Resistance Susceptible Susceptible
11	Djiappi-Tchamen et al. 2021	Douala, Cameroon	DDT Permethrin Deltamethrin	Organochlorine Pyrethroid Pyrethroid	High Resistance High Resistance High Resistance

12	Rasli et al. 2021	Selangor, Malaysia	Permethrin	Pyrethroid	High Resistance
			Deltamethrin	Pyrethroid	High Resistance
			Malathion	Organophosphate	High Resistance
13	Fernando et al. 2020	Sri Lanka	Permethrin	Pyrethroid	High Resistance
			Deltamethrin	Pyrethroid	High Resistance
			Temephos	Organophosphate	High Resistance
14	Saeung et al. 2020	Thiland	Temephos	Organophosphate	Moderate Resistance
	Al-Amin et al. 2020	Dhaka, Bangladesh	Permethrin	Pyrethroid	High Resistance
15			Deltamethrin	Pyrethroid	Moderate Resistance
			Malathion	Organophosphate	Moderate Resistance
			Bendiocarb	Carbamate	Susceptible
16	Guedes et al. 2020	Latin America and the Caribbean	DDT	Organochlorine	High Resistance
			Temephos	Organophosphate	Moderate Resistance
			Deltamethrin	Pyrethroid	Low Resistance
17	Morales et al. 2019	Ecuador	Deltamethrin	Pyrethroid	High Resistance
			Malathion	Organophosphate	Susceptible
			Temephos	Organophosphate	Low Resistance
18	Demok et al. 2019	Papua New Guinea	Deltamethrin	Pyrethroid	Susceptible
			Malathion	Organophosphate	Susceptible
			Bendiocarb	Carbamate	Susceptible
			Lambda-cyhalothrin	Pyrethroid	Susceptible
			DDT	Organochlorine	Moderate Resistance
19	Sombié et al. 2019	Burkina Faso	Bendiocarb	Carbamate	High Resistance
			Propoxur	Carbamate	High Resistance
			Permethrin	Pyrethroid	High Resistance
			Deltamethrin	Pyrethroid	High Resistance
			Fenitrothion	Organophosphate	Susceptible
			Malathion	Organophosphate	Susceptible
20	Bharati and Saha 2018	West Bengal, India	Permethrin	Pyrethroid	Moderate Resistance
			Deltamethrin	Pyrethroid	Susceptible
			Lambda-cyhalothrin	Pyrethroid	Susceptible
			DDT	Organochlorine	High Resistance
			Malathion	Organophosphate	Moderate Resistance
			Propoxur	Carbamate	Moderate Resistance
21	Samal and Kumar, 2018	New Delhi, India	Acetamidrid	Neonicotinoids	Low Resistance
22	Garcia et al. 2018	Brazil	Deltamethrin	Pyrethroid	High Resistance
23			Temephos	Organophosphate	Moderate Resistance
24	Estep et al. 2018	Florida, USA	Permethrin	Pyrethroid	High Resistance
25	Goindin et al. 2017	Guadeloupe and Saint Martin islands (French West Indies)	Deltamethrin	Pyrethroid	Moderate Resistance
			Temephos	Organophosphate	High Resistance
			Malathion	Organophosphate	Low Resistance
26	Seixas et al. 2017	Madeira Island, Portugal	Bendiocarb	Carbamate	High Resistance
			Fenitrothion	Organophosphate	High Resistance
			Permethrin	Pyrethroid	High Resistance
			Cyfluthrin	Pyrethroid	High Resistance
27	Mathias et al. 2017	Tanzania	Deltamethrin	Pyrethroid	Low Resistance
			Permethrin	Pyrethroid	Low Resistance
			Lambda-cyhalothrin	Pyrethroid	Low Resistance
28	Chediak et al. 2016	Brazil	Temephos	Organophosphate	High Resistance
29	Suzuki et al. 2016	Ghana	Deltamethrin	Pyrethroid	High Resistance
			Permethrin	Pyrethroid	Susceptible
			DDT	Organochlorine	High Resistance
			Lambda-cyhalothrin	Pyrethroid	Low Resistance
30	Ayorinde et al. 2015	Nigeria	DDT	Organochlorine	High Resistance
			Deltamethrin	Pyrethroid	Susceptible
			Permethrin	Pyrethroid	Susceptible
31	Sivan et al. 2015	Andaman and Nicobar Islands, India	DDT	Organochlorine	High Resistance
			Fenitrothion	Organophosphate	High Resistance
			Malathion	Organophosphate	Susceptible
			Bendiocarb	Carbamate	High Resistance
			Propoxur	Carbamate	Susceptible
			Deltamethrin	Pyrethroid	Susceptible
			Permethrin	Pyrethroid	High Resistance
			Lambda-cyhalothrin	Pyrethroid	Low Resistance
32	Li et al. 2015	Southern China	Cypermethrin	Pyrethroid	High Resistance
			Cyhalothrin	Pyrethroid	High Resistance
33	Uragayala et al., 2015	India	Imidacloprid	Neonicotinoid	Susceptible
34	Astuti et al. 2014	West Java, Indonesia	Cypermethrin	Pyrethroid	Susceptible
35	Maestre-Serrano et al.	Colombian Caribbean	Temephos	Organophosphate	Low Resistance

	2014	Region	Malathion	Organophosphate	Susceptible
			Fenitrothion	Organophosphate	Susceptible
36	Aponte et al. 2013	Mexico	DDT	Organochlorine	High Resistance
			Deltamethrin	Pyrethroid	High Resistance
			Permethrin	Pyrethroid	High Resistance
37			DDT	Organochlorine	High Resistance
			Deltamethrin	Pyrethroid	High Resistance
	Darriet and Chandre, 2013	Vietnam	Acetamiprid	Neonicotinoid	Low Resistance
			Nitenpyram	Neonicotinoid	Low Resistance
			Thiamethoxam	Neonicotinoid	Low Resistance
			Clothianidin	Neonicotinoid	Low Resistance
			Imidacloprid	Neonicotinoid	Low Resistance
			Thiacloprid	Neonicotinoid	Low Resistance
38	Dia et al. 2012	Senegal	Fenitrothion	Organophosphate	Susceptible
			Permethrin	Pyrethroid	Susceptible
			Deltamethrin	Pyrethroid	Low Resistance
			Lambda-cyhalothrin	Pyrethroid	Low Resistance
			Propoxur	Carbamate	Low Resistance
39	Martins et al. 2012	Brazil	Deltamethrin	Pyrethroid	High Resistance
40	Marcombe et al. 2011	Island of Martinique (Caribbean)	Deltamethrin	Pyrethroid	High Resistance
41	Polson et al. 2011	Trinidad and Tobago	DDT	Organochlorine	High Resistance
			Deltamethrin	Pyrethroid	Low Resistance
			Permethrin	Pyrethroid	Low Resistance
42			Cyfluthrin	Pyrethroid	Susceptible
			Deltamethrin	Pyrethroid	Susceptible
			Lambda-cyhalothrin	Pyrethroid	Moderate Resistance
	Fonseca-González et al. 2011	Colombia	Permethrin	Pyrethroid	Moderate Resistance
			Malathion	Organophosphate	Susceptible
			Fenitrothion	Organophosphate	High Resistance
			DDT	Organochlorine	High Resistance
43	Kamgang et al. 2011	Cameroon	Temephos	Organophosphate	Susceptible
			Deltamethrin	Pyrethroid	Low Resistance
			Fenitrothion	Organophosphate	Susceptible
			Propoxur	Carbamate	Susceptible
			DDT	Organochlorine	High Resistance
44	Husham et al. 2010	Sudan	Malathion	Organophosphate	High Resistance
			Lambda-cyhalothrin	Pyrethroid	Low Resistance
			Deltamethrin	Pyrethroid	Susceptible
			Bendiocarb	Carbamate	Susceptible
			DDT	Organochlorine	High Resistance

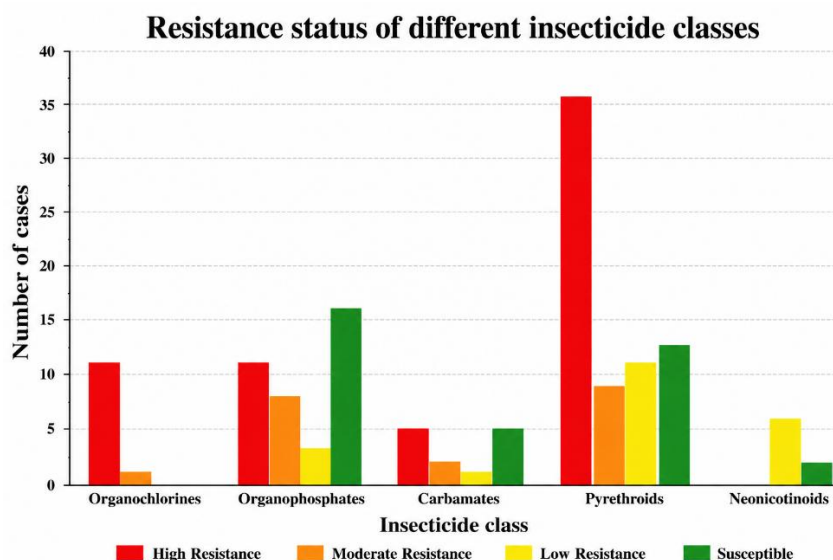


Fig. 1: Insecticide Resistance by class

Mechanisms of Insecticide Resistance

The development of insecticide resistance is a complex phenomenon that is directly influenced by genetic, physiological, behavioral, and ecological factors, and indirectly shaped by the intensity and frequency of insecticide use (Figure-2, Table-2) (Zhu *et al.*, 2016). Prolonged and repeated use of the same insecticide can lead to the development of resistance in insect populations that are consistently exposed to it. For instance, *Aedes aegypti* (L.) in the Americas has demonstrated notable resistance to temephos, whereas reports of temephos resistance in the Asian region are relatively limited. (Hemingway and Ranson 2000; Wirth and Georgiou 1999; Chareonviriyaphap *et al.* 1999). Four primary types of resistance mechanisms have been identified based on biochemical processes:

Altered target-site resistance

Insects primarily develop target site insensitivity through non-silent point mutations in structural genes. Nevertheless, only a few specific alterations can reduce sensitivity to insecticides without interfering with the normal physiological functions of the target site (Karunaratne, 1998; Hemingway *et al.*, 2004). Target site resistance in mosquitoes is caused by single or multiple mutations in specific target genes, such as the voltage-gated sodium channel (VGSC) gene associated with knockdown resistance (kdr), as well as mutations in the acetylcholinesterase (Ace-1) gene and GABA receptors (Ishak *et al.*, 2017; Enayati *et al.*, 2003). Pyrethroid resistance in insects is referred to as knockdown resistance (kdr), which arises from mutations in the voltage-gated sodium channel (VGSC)—the primary target site for both DDT and pyrethroid insecticides (Brogdon *et al.*, 1999; Uemura *et al.*, 2024). When the three mutations V1016G, S989P, and F1534C occur together, they can lead to much stronger resistance to pyrethroids, as seen in *Aedes aegypti* mosquitoes from Myanmar (Kawada *et al.*, 2014). The kdr mutation modifies the binding site for insecticide molecules in the pyrethroid and DDT (dichlorodiphenyltrichloroethane) classes, reducing their effectiveness in controlling mosquito populations. Additionally, resistance can be associated with mutations in the Ace-1 gene, which lead to reduced susceptibility to organophosphate and carbamate insecticides, including malathion and temephos (Samal *et al.*, 2022). In Indonesia, the most frequently observed kdr mutations are V1016G and F1534C, both of which play a significant role in conferring resistance to pyrethroid insecticides (Sayono *et al.*, 2016). Hamid *et al.*, (2020) showed that the V1016G mutation in the *Aedes aegypti* population from Makassar, Indonesia was linked to resistance against permethrin. The removal of insecticides does not immediately reverse

resistance in a given area, as resistance genotypes can continue to persist even after the agent responsible for inducing the mutations has been removed (Macoris *et al.*, 2018).

Metabolic resistance

Metabolic resistance in *Ae. aegypti* involves changes in enzyme expression that enhance insecticide detoxification, primarily through GSTs, esterases, and cytochrome P450 monooxygenases. A global genome project identified 160 P450 genes, 49 GSTs, and 26 esterases in this species (Strode *et al.*, 2008). Esterases confer resistance to organophosphates (temephos), carbamates, and pyrethroids (due to their ester bonds) (Grigoraki *et al.*, 2016; Li *et al.*, 2007). Glutathione S-transferases (GSTs) provide resistance to organochlorines (DDT), organophosphates, and pyrethroids (Li *et al.*, 2007; Hemingway and Ranson, 2000). In *Aedes aegypti*, the GST-based resistance mechanism is likely driven by a trans-acting regulatory factor, which also play a role in mitigating insecticide-induced oxidative stress (Ranson *et al.*, 2001; Ding *et al.*, 2005). Monooxygenases (cytochrome P450s) participate in the breakdown of nearly all types of insecticides. Elevated expression of P450 genes leads to higher overall levels of P450 enzymes, which in turn contributes to insecticide resistance (Gong *et al.*, 2013). However, identifying the enzymes associated with insecticide resistance is challenging due to the diverse range of P450 genes and the high structural similarity among their isoforms, making it difficult to pinpoint the specific isoforms related to resistance (Marcombe *et al.*, 2009). Studying metabolically driven insecticide resistance to pyrethroids in *Ae. aegypti* is crucial, as multiple resistance mechanisms often exist simultaneously (Amelia-Yap *et al.*, 2018)

Penetration resistance

Reduced insecticide penetration primarily results from structural changes in the insect cuticle, such as thickening, which slows down the absorption and entry of insecticides, thereby lowering their overall uptake (Ondeto *et al.*, 2017; Zhu *et al.*, 2016). This reduced penetration allows metabolic enzymes more time to detoxify the insecticides. Since most insecticides are lipophilic, cuticular resistance often leads to cross-resistance against various insecticide types. (Scott, 1989; Nkya *et al.*, 2013). Overexpression of cytochrome P450 enzymes, particularly CYP4G16 and CYP4G17, enhances cuticular hydrocarbon production in highly pyrethroid-resistant *Aedes aegypti*. This leads to increased hydrocarbon deposits in the epicuticle, reducing insecticide penetration. Studies suggest that this cuticular resistance, indicated by slower ¹⁴C-deltamethrin absorption, is linked to elevated P450

monooxygenase expression (Kasai et al., 2014; Balabanidou et al., 2016; Bass and Jones, 2016).

Behavioral resistance

Behavioral resistance happens when mosquitoes change their behavior to avoid coming into contact with insecticides or toxic substances, helping them or their offspring survive. Even though it plays an important role, this type of resistance is often overlooked

(Chareonviriyaphap et al., 2013; Pittendrigh et al., 2013). Insects that have developed behavioral resistance can sense the presence of insecticides in their surroundings and relocate to a safer area (Gatton et al., 2013). *Aedes* mosquitoes can adapt to minimize the harmful effects of insecticides by either escaping after coming into contact with a treated surface or avoiding the insecticide-exposed area altogether before any contact occurs (Amelia-Yap et al., 2018).

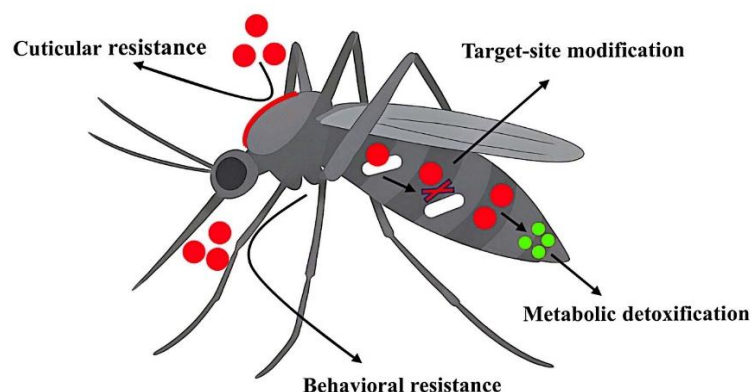


Fig. 2: Schematic diagram of a mosquito outlining different modes of insecticides resistance

Table-2: Brief details of resistance mechanisms in *Aedes aegypti*

Sl. No.	References	Location	kdr Mutation	Metabolic Resistance	Resistant to Insecticides
1	Massa et al., 2025	Nouakchott, Mauritania	S989P, V1016G, and F1534C	-	Permethrin and Deltamethrin
2	Estep et al., 2025	Florida, USA	V1016I and F1534C	-	Permethrin and Deltamethrin
3	Chen et al., 2024	China-Myanmar border	S989P, V1016G, and F1534C	-	Permethrin, Lambda-cyhalothrin, and Deltamethrin
4	Parker-Crockett et al., 2021	Orlando, USA	V1016I and F1534C	-	Pyrethroids
5	Rahman et al., 2021	Lahore, Pakistan	T1520I and F1534C	PBO	Pyrethroids
6	Chen et al., 2021	Florida, USA	V1016I and F1534C	-	Permethrin
7	Kushwah et al., 2020	Bengaluru, India	F1534L, S989P, F1543C, and V1016G	-	Pyrethroids
8	Sombié et al. 2019	Burkina Faso	V1016I and F1534C	-	Pyrethroid and Carbamate
9	Bharati and Saha 2018	West Bengal, India	-	Carboxylesterase	Organophosphate
10	Seixas et al. 2017	Madeira	F1534C and V1016I	MFO, Esterases, PBO, and DEM	Pyrethroids and Carbamates
11	Kamgang et al., 2017	Cameroon and Gabon	-	PBO	Pyrethroids, Carbamates, and DDT
12	Kawada et al., 2016	Ghana	F1534C and V1016I	-	Pyrethroids and DDT
13	Ngoagouni et al., 2016		-	MFO, Esterases, GSTs	Deltamethrin and DDT
14	Kushwah et al., 2015	Delhi, India	F1534C and T1520I	-	Organochlorine and Pyrethroids
15	Rocha et al., 2015	Cape Verde	-	MFO, Esterases, GSTs	Pyrethroids
16	Li et al., 2015		S989P and V1016G	-	Cypermethrin and Cyhalothrin
17	Ishak et al., 2015	Malaysia	F1534C and V1016G	-	pyrethroids, DDT, Temephos, and bendiocarb
18	Muthusamy and Shivakumar, 2015	Tamil Nadu, India	-	MFO, Esterases,	Organophosphate
19	Martins et al., 2009	Brazil	V1016I	-	Deltamethrin
20	Chang et al., 2009	Taiwan	D1794Y, V1016G	-	Permethrin
21	Saavedra-Rodríguez et al., 2007	Cuba and Mexico	V1016I, I1011V	-	Permethrin and Deltamethrin
22	Brengues et al., 2003	Brazil, Indonesia and Vietnam	I1011M, G923V, V1016G, and L982W	-	DDT and Pyrethroids

MFO (mixedfunctionoxidases); PBO (piperonylbutoxide); DEM (diethylmaleate); GSTs (glutathioneS-transferase).

Strategies to Manage and Mitigate Resistance

The failure of vector control efforts due to *Aedes aegypti* resistance significantly increases costs, primarily because of the need for repeated insecticide use, multiple rounds of spraying, and ongoing treatments—particularly in areas with limited infrastructure (Palumbi 2001). Effective insecticide management can help delay

the development of resistance (Figure-3). This can be achieved by raising community awareness, integrating various chemical strategies, and incorporating the use of bioinsecticides (Hamid et al., 2020). Insecticides derived from natural sources are considered a safer and more environmentally friendly option for both humans and nature (De Souza Wuillda et al., 2019).

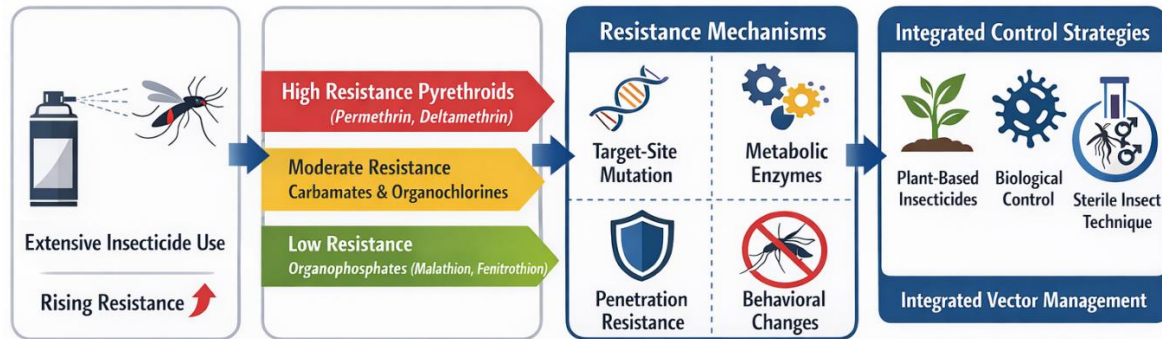


Fig. 3: Insecticide resistance in dengue vector *Aedes aegypti*: Status, Mechanisms & Control.

Plant-based control

The current trend in vector control is shifting towards the use of plant-based substances, as they are cost-effective and abundant in bioactive compounds. Since ancient times, humans have relied on a wide variety of plants containing toxic chemicals to manage mosquito populations, highlighting nature's potential as a valuable source for mosquito control agents. (Siam et al., 2021, Siam et al., 2022). Plant extracts and essential oils have long been studied and utilized as mosquito insecticides because their compounds can act on multiple targets, thereby boosting their overall insecticidal effectiveness (Mendez-Sanchez et al., 2021).

Luker et al. (2023) reported that lotion emulsions containing 10% v/v of either clove oil or cinnamon oil offered the most prolonged protection against bites from *Aedes aegypti* mosquitoes. *Areca catechu*, *Azolla pinnata*, *Lantana camara*, *Mukia maderaspatana*, and *Leucas aspera* contain key compounds like fatty acids, their methyl esters, and flavonoids like catechin. These biodegradable compounds are patented in pesticide formulations for enhancing effectiveness (Bharathithasan et al., 2024). The leaf extracts of *Justicia adhatoda* L. (Acanthaceae) and the crude metabolic extracts of *Acanthospermum hispidum* both exhibited mosquitocidal activity, highlighting their potential as natural larvicidal agents against *Aedes aegypti*. (Thanigaivel et al., 2017; Vivekanandhan et al., 2018). Essential oils derived from plants in the Lamiaceae and Zingiberaceae families exhibited bioactivity against *Aedes aegypti* (Kalaivani et al., 2012), while the crude volatile oil from *Piper betle* leaves

showed notable larvicidal, oviposition-deterrent, and repellent effects against the same mosquito species (Vasanth-Srinivasan et al., 2018).

Unlike synthetic chemicals, plant-based compounds have not shown evidence of resistance development, likely due to their mix of multiple bioactive components with varied modes of action, making it harder for mosquitoes to adapt (Mulla and Su, 1999; Shaalan et al., 2005).

Biological Control

Biological control (biocontrol) involves using an organism's natural enemies—such as predators, parasites, or pathogens—to help manage and reduce its population. One widely studied biocontrol approach involves using larvivorous arthropods that prey on mosquito larvae. *Toxorhynchites rutilus rutilus* (Diptera: Culicidae), a species native to the southeastern U.S., has been tested in field trials in Louisiana, where it achieved an average of 74% control of *Aedes aegypti* populations in New Orleans (Focks et al. 1982). Another biocontrol method for mosquito management involves the use of larvivorous fish, such as mosquito fish (*Gambusia* spp.) and killifish (*Fundulus* spp.), which are particularly effective in larger water bodies like cisterns and wells where *Aedes aegypti* may breed (LeVan 1941).

The microsporidian *Edhazardia aedis* (Kudo) has shown potential as a biological control agent for *Aedes aegypti*. Laboratory studies have demonstrated its ability to transmit vertically from mother to offspring, significantly reducing egg batch size and adult

emergence rates (Becnel et al., 1995). Entomopathogenic fungi like *Beauveria bassiana* and *Metarhizium anisopliae* show strong potential as alternative methods for mosquito control (Darbro et al., 2012). In laboratory settings, *B. bassiana* has been shown to reduce the lifespan of *Aedes aegypti*, while semi-field experiments reported decreased fecundity, adult survival, and blood-feeding in infected mosquitoes. Similarly, *M. anisopliae* has demonstrated well-established larvicidal and adulticidal effects against *Aedes* species (Scholte et al., 2007). *Bacillus thuringiensis israelensis* is a widely used bacterium that, once ingested by mosquito larvae, produces toxins that damage their stomach lining, leading to death either by starvation or septicemia (Gill et al., 1992).

Sterile Insect Technique

Sterile Insect Technique (SIT) involves releasing sterilized male insects in large numbers to outcompete fertile males, resulting in infertile matings and reduced mosquito populations, as females typically produce nonviable offspring and may not mate again (Dyck et al. 2005). A novel method using RNA interference (RNAi) has been developed to produce sterile male *Aedes aegypti* without radiation (Hannon, 2002). By feeding larvae double-stranded RNA (dsRNA) targeting testis and female sex determination genes, Whyard et al. achieved reduced male fertility and a male-skewed population (Whyard et al., 2015)

Mechanical control

Trapping is often underestimated as a control method due to labor demands and low catch rates. While tools like ovitraps, BG Sentinel traps, and CDC light traps are mainly used for surveillance, recent improvements have enhanced their mosquito capture and kill efficiency, expanding their role from monitoring to active control (Kline 2006). Ovitrap traps take advantage of *Aedes* mosquitoes' tendency to lay eggs in small containers, serving as a cost-effective, passive, and sensitive tool for monitoring the presence of container-breeding mosquitoes and tracking adult population trends (Dowling et al., 2013). Field trials with lethal ovitraps in Brazil, Peru, and Thailand demonstrated effective reductions in *Aedes aegypti* population density. However, the impact was less pronounced in Thailand, likely due to the abundance of water containers near homes (Zeichner and Debboun, 2011; Perich et al., 2003). Research has demonstrated that BG-Sentinel traps, particularly when supplemented with a CO₂ source, are highly effective at capturing *Aedes* species mosquitoes (Ázara et al., 2013). In Brazil, Degener et al. (2014) reported that large-scale deployment of BG-Sentinel traps, even without attractant lures, led to a significant decrease in adult *Aedes aegypti* populations.

5.5. Chemical control: The most common way to control *Aedes aegypti* mosquitoes is through the use of insecticides. The World Health Organization recommends several main types, including organochlorines, organophosphates, carbamates, and pyrethroids (WHO, 2011). From figure 2&3, it is evident that organophosphates, particularly malathion and fenitrothion, still exhibit some effectiveness against the *Aedes aegypti* vector. Insect growth regulators (IGRs) like pyriproxyfen, methoprene, and diflubenzuron are widely used larvicides available in various commercial formulations. In addition to targeting larvae, they also exhibit ovicidal properties by inhibiting egg hatching, depending on their mode of action, dosage, and the mosquito species involved (Suman et al., 2013). IGRs are considered relatively safe for non-target organisms (Mulla, 1995).

Conclusion

This review presents an updated overview of the insecticide resistance status and underlying resistance mechanisms in *Aedes aegypti* mosquitoes against the four main classes of insecticides: pyrethroids, organochlorines, organophosphates, and carbamates. *Aedes* mosquitoes exhibit the highest level of resistance to pyrethroid insecticides, especially permethrin and deltamethrin, while showing the greatest susceptibility to organophosphates, particularly malathion and fenitrothion. Understanding the emergence of resistance in dengue vectors can help refine policies more effectively, aiming to reduce resistance caused by the localized use of insecticides in dengue control programs. A multidisciplinary approach to controlling *Aedes* mosquitoes, incorporating non insecticidal methods such as plant-based products, biological control, mechanical control, and sterile insect techniques, can serve as effective alternatives to synthetic insecticides.

Author contributions

The study was designed and conceptualized by M. A. Habib Siam. Articles from online resources were downloaded by M. A. Habib Siam. Data analysis were carried out by M. A. Habib Siam and J.K. Owaresat. Manuscript was written by M. A. Habib Siam and revised by D. Dey. Each author made significant contributions to the final version of the paper.

Competing Interests

The authors declare no conflict of interest to the research, authorship, and publication of this article.

Ethics approval and consent to participate

This research does not contain any studies with human participants.

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Compliance with ethical standards

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Data availability statement

The data supporting the findings of this study are provided in the tables within this manuscript.

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